

University of Groningen

Effects of intake rate on energy expenditure, somatic repair and reproduction of zebra finches

Wiersma, Popko; Verhulst, Simon

Published in:
The Journal of Experimental Biology

DOI:
[10.1242/jeb.01854](https://doi.org/10.1242/jeb.01854)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2005

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Wiersma, P., & Verhulst, S. (2005). Effects of intake rate on energy expenditure, somatic repair and reproduction of zebra finches. *The Journal of Experimental Biology*, 208(21), 4091-4098.
<https://doi.org/10.1242/jeb.01854>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Effects of intake rate on energy expenditure, somatic repair and reproduction of zebra finches

Popko Wiersma* and Simon Verhulst

Zoological Laboratory, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

*Author for correspondence at present address: Department Evolution, Ecology and Organismal Biology, Ohio State University, 288 Aronoff Lab, 318 W 12th Avenue, Columbus, OH 43210, USA (e-mail: wiersma.6@osu.edu)

Accepted 23 August 2005

Summary

Understanding the effect of food availability on food requirements is critical when linking food availability e.g. to reproduction or habitat selection. Decreasing intake rate (intake per unit foraging effort) can be expected to increase daily energy expenditure (DEE), due to increased foraging costs. However, all the studies we could find that have tested this hypothesis (with one exception) found DEE to be constant or decreasing when intake rate was experimentally decreased. This may be due to the design of the reward schedule, which can be fixed (e.g. 20 units effort required for each reward) or variable (e.g. each unit effort rewarded with probability 1/20). Most studies used fixed reward rates, but foraging motivation is generally higher for variable reward rates, and the only study in which animals increased DEE when intake rate decreased used variable reward rates. To assess the generality of this result, we exposed zebra finches *Taeniopygia guttata* to different intake rates using variable reward rates. We decreased intake rate by mixing 25 g of seeds with 0, 25 or 75 g of chaff. With increasing chaff/seed ratio the time spent foraging increased from 6% to 27%, but this was insufficient to compensate for the lower intake rate, because DEE decreased by 6.6%. Body mass was independent of chaff/seed ratio. Effects of intake rate on foraging time and DEE were stronger at lower

temperatures, when DEE was higher. The decrease in DEE in adverse conditions raises the question of what prevents such behaviour in benign circumstances.

We hypothesize that energy is saved at the expense of 'condition', and we tested this hypothesis in two ways. Firstly, we tested the effect of intake rate on the replacement of two plucked tail feathers (a form of somatic repair). Replacement feathers were shorter when intake rate was low, indicating an effect of intake rate on somatic repair ability. Secondly, we tested for carry-over effects of intake rate on reproduction, by giving pairs the opportunity to reproduce with access *ad libitum* to food after feeding on one of the three chaff/seed ratios for 6 weeks. The interval until laying the first egg increased with decreasing intake rate in the preceding 6 weeks. The effects of intake rate on somatic maintenance and reproduction may explain why birds sustained higher metabolic rates than apparently necessary, but the physiological mechanisms determining the optimal metabolic rate remain to be discovered.

Key words: food availability, basal metabolic rate, ptilochronology, *Taeniopygia guttata*.

Introduction

Resource availability for reproduction is the surplus of energy gain over and above the energy allocated to foraging and somatic maintenance, and consequently knowledge of effects of intake rates on the energy budget may provide insights into life-history decisions. Recent studies indicate that the relationship between intake rate (energy gain per unit foraging effort) and energy expenditure may not be clearcut. Deerenberg et al. (1998) manipulated net intake rate of zebra finches that earned their food by hopping between two perches, and found that daily energy expenditure (DEE) decreased when the effort required per reward was increased. Bautista et al. (1998) obtained the same result in comparable experiments with starlings. This result is surprising because, everything else remaining constant, an increase in energy allocated to foraging

would result in an increase in DEE (see also the accompanying paper, Wiersma et al., 2005).

An explanation for this counterintuitive result may lie in the structure of the reward schedule, because in starlings the foraging motivation depends on the variation in reward rate: when food was earned by performing a fixed number of flights, daily food intake and body mass decreased when the number of flights required per reward was increased, while within a trial both remained constant when the number of flights needed to obtain a reward was variable (Fotheringham, 1998). Hence, identical mean foraging intake rates that differ only in short-term variation around the mean may result in very different energy budgets (see discussion in Kacelnik and Bateson, 1996). Thus the findings of Deerenberg et al. (1998) and Bautista et

al. (1998) that DEE decreased with decreasing intake rates may be explained by the use of fixed reward rates in these studies. Indeed, Wiersma et al. (2005) offered starlings variable reward rates and showed an increase in DEE when foraging costs were increased beyond those used by Fotheringham (1998). In this paper we test whether zebra finches (like the starlings) increase DEE with decreasing intake rate when foraging reward rate is variable. We further explore the consequences of intake rate for reproduction and an aspect of somatic repair.

Following Lemon (1991), we created lower intake rates by mixing seeds with increasing amounts of chaff. In this foraging environment the reward rate is variable, and we therefore predicted that DEE would increase with increasing chaff/seed ratio. Lemon (1991) previously showed that fitness was lower when more chaff was mixed through the seeds (see also Spencer et al., 2003), and he constructed an energy budget to explain this result. Although intake rate was strongly affected by the treatment, Lemon (1993) did not find differences in DEE between the experimental groups. However, he constructed energy budgets indirectly, using a summation of separately measured existence metabolism values of fasting birds and foraging costs, and if nocturnal savings occurred (as in Deerenberg et al., 1998) these may have concealed differences in diurnal energy expenditure. Therefore, we used respirometry to measure effects of food intake rates on energy expenditure separately for the diurnal and nocturnal phase.

The conditional occurrence of energetic compensation begs the question what the costs are to a reduction in metabolic rate below levels found under benign conditions. Possibly, energy is saved by reallocation to foraging from maintenance and repair processes (e.g. oxidative protection, Wiersma et al., 2004; or immune function, Verhulst et al., 2005). As an indicator of resource allocation to somatic repair, we tested whether induced feather growth was affected by foraging costs. This method has previously been shown to reveal nutritional stress and effects of parental effort (e.g. Grubb, Jr et al., 1991; White et al., 1991; Nilsson et al., 1993; Jenkins et al., 2001). Additionally, we tested for carry-over effects of manipulated foraging costs on reproductive output by giving birds the opportunity to breed after being exposed for 6 weeks to different levels of intake rate. Lemon (1991) previously showed that reproductive success, in particular the laying interval between successive clutches, depends on intake rate, but his birds were permanently exposed to the different treatments. His finding may therefore be the combined result of instantaneous effects of the daily energy surplus and longer term effects on parental condition that affect reproduction, and we tested the latter hypothesis. Lastly, to evaluate the generality of our findings regarding effects of intake rate on DEE, we provide an overview of studies that manipulated intake rate and measured the consequences for foraging effort, daily energy expenditure and basal metabolic rate.

Materials and methods

We applied three different treatments, mixing 25 g seeds

with 0, 25 or 75 g of chaff, respectively. A new batch of the chaff/seed mixture was provided every other day and drinking water was available continuously. Zebra finches *Taeniopygia guttata* Vieillot were housed in single-sex pairs in cages measuring 40 cm × 80 cm × 40 cm (height × width × depth). Ambient temperature was between 22 and 24°C and lights were on for 10 h per day.

Experiment 1: Feeding time and energetics

Twelve single-sex pairs of wild-type zebra finches (6 pairs of each sex) were all subjected to the three different chaff/seed ratios. After 1 week of acclimatization on a particular chaff/seed ratio we measured energy expenditure for 22–23 h in an open-flow respirometer, and this was repeated at three different temperatures (12, 22 and 32°C) at 3-day intervals. During these measurements the pair had access to food in the same chaff/seed ratio as in the preceding week. According to Calder (1964), 32°C is within the thermoneutral zone; 22°C resembles the temperature in the holding room; measurements at 12°C served to test whether nocturnal saving depended on overall energetic demands. After measuring metabolic rate at the three ambient temperatures the chaff/seed ratio for that pair was changed, and the procedure was repeated. We arranged the order of chaff/seed ratios and measurement temperatures in such a way that treatments and measurement order were not correlated.

The metabolic measurements were done on the two birds of a pair simultaneously, for several reasons: (i) to increase oxygen consumption rates, and hence measurement precision, (ii) to reduce the variance between measurements, because some averaging is taking place, which increases the statistical power, and (iii) because the zebra finch is a gregarious species, it may be more at ease when housed with a conspecific. Although individual variation becomes less clear with this approach, we considered it preferable because of the advantages mentioned. Significant repeatability of resting metabolic rate (RMR) has previously been demonstrated for the zebra finch (Vézina and Williams, 2005). In the metabolic chamber the two birds were separated by a transparent partition, so they could see and hear each other but not interact physically. Measurements of oxygen consumption (using a paramagnetic Servomex Xentra 4100 analyzer, Crowborough, UK), carbon dioxide production (Servomex 1440) and air flow rate (Brooks 5850S mass-flow controllers, Rijswijk, The Netherlands) were stored every sixth minute. Mass-flow controllers had been calibrated using a bubble flow meter (Levy, 1964). The respirometer system was calibrated before each measurement using two 3-digit precision gas mixtures (N₂ with 20.0% O₂/0.0% CO₂ or 21.0% O₂/1.0% CO₂). Dry air was pumped through the 24 l, Plexiglas respirometer boxes at a rate of 36 l h⁻¹. The air was dried over a molecular sieve (3Å, Merck, Darmstadt, Germany). The metabolic rate (MR) was calculated from the oxygen consumption rate using the RQ-dependent conversion factor as given by Brody (1945). All MR measurements were divided by 2 to obtain values per bird. Before and after the measurement we measured body mass to

the nearest 0.1 g. BMR was defined as the minimum metabolic rate at thermoneutral temperatures measured during the resting phase of post-absorptive birds. Since measurements did not cover the whole daylight period (2–3 h were missing in the middle of the day due to time needed to exchange birds and for the respirometer system to stabilise), we used the average of the end and start of the measurement as an estimate for the missing period to estimate energy expenditure over the whole daylight period.

From a subset of respirometry sessions ($N=45$) we made 1.5 h video recordings of the feeding behaviour of single birds, starting at the onset of the light period (9:00 h). Due to the position of the camera we could not observe the whole metabolic chamber, and when analyzing the video recordings we only scored the time spent foraging. Activity (presence/absence of movement) was recorded continuously with passive infrared sensors (PIRs) in the metabolic chambers. The PIRs did not distinguish between the two individuals. PIRs sampled movement approximately every second, and 'activity' was defined as the proportion of samples with movement. Individual sensors differed in sampling rate, and therefore we corrected for the maximum output of all measurements made by individual PIRs. Pairs were always measured in the same chamber.

Experiment 2: Feather growth and reproduction

Following the metabolic measurements we formed 24 female–male pairs, which were each maintained on one of the three chaff/seed ratios for 6 weeks (8 pairs for each seed/chaff ratio). We measured the amount of food consumed by weighing the seeds remaining in the food tray 48 h after presenting the food. This was repeated twice more at weekly intervals. We removed the left and right outer tail feathers of 12 pairs at the start of the 6 weeks. Length of the new feathers was measured using a ruler 12 days after feather removal by an observer who was 'blind' with respect to the treatment, and subsequently at 4–8 day intervals. We took the maximum recorded new feather length as an estimate of the length of the newly formed feather. 6 weeks after feather removal the new feathers had ceased to grow and the newly formed feathers were removed and measured.

After 6 weeks all 24 pairs were given a diet with seeds only (i.e. no chaff) and a nest box and nesting material to measure carry-over effects of the chaff/seed ratio on subsequent reproductive output. We recorded day of laying the first egg, clutch size, egg mass, brood size and fledgling number. The first 3 days after the diet switch we measured seed consumption by reweighing the offered seeds at 24 h intervals.

Statistical analyses

We used Generalized Linear Models (GLM), or, when repeated measurements were collected on the pairs, Generalized Linear Mixed Models (GLMM) with a pair identifier (i.e. cage number) on the first level. Because video observations were done on the individual birds of the pairs inside the respirometer box, models including observational

data used average individual MRs (i.e. two birds of a pair obtained same MR value). On the subset of respirometer measurements we collected 74 observational data points for 24 individuals. Models excluding observational data used one MR and body mass data point per pair (i.e. 106 cases; 12 pairs \times 3 treatments \times 3 temperatures, minus 2 data points due to technical failure respirometer). Statistically significant variables (including two-way interactions) were selected using stepwise backward deletion of non-significant variables. Chaff/seed ratio was entered as a covariate, with values 0, 1 or 3. To test for nonlinearity we entered chaff/seed-squared and temperature-squared in the models, but these never yielded significant results. All tests were two-tailed, except for the tests of treatment effect in experiment 2 on feather growth and laying interval (P -values denoted by P_1), because previous food manipulations had all yielded either no effect, or reduced feather growth (e.g. Grubb, Jr et al., 1991; White et al., 1991; Nilsson et al., 1993; Jenkins et al., 2001) and/or increased laying intervals (Lemon, 1991; Deerenberg and Overkamp, 1999).

Results

Experiment 1

Feeding time and energetics

Time spent foraging increased with increasing chaff/seed ratio, in particular at low temperatures (Fig. 1; see figure legend for statistical details). Up to 50% of time was spent foraging when both temperature and food availability were low, while only 5% of time was spent foraging when both temperature and food availability were high. Although foraging time always increased with increasing chaff/seed ratio, total activity decreased with increasing chaff/seed ratio in all comparisons except when chaff/seed ratio increased from 1 to 3 at 12°C (Fig. 1B). This indicates a strong decrease in activity during the time that birds were not foraging.

DEE decreased with increasing chaff/seed ratio and was higher at lower temperatures (Fig. 2). The effect of chaff/seed ratio on DEE was not due to body mass variation, because body mass was independent of chaff/seed ratio (Fig. 1C). Moreover, the treatment effect on DEE remained significant when average mass of the pair was added to the model. The treatment effect on DEE was due to a reduction in both diurnal and nocturnal energy expenditure (Fig. 3). The nocturnal reduction of chaff/seed ratio was stronger at low temperatures, while the diurnal reduction was independent of temperature. As for DEE, the treatment effects were not due to effects on body mass, because they remained significant when body mass was added to the models. For all three analyses (DEE, diurnal and nocturnal metabolic rate) the same results emerged when metabolic rate was expressed per gram.

Nocturnal metabolic rate over the whole night does not necessarily reveal the same patterns as the lowest recorded metabolic rate in a night (i.e. basal or standard metabolic rate), because foraging conditions can have an effect on the nocturnal metabolic profile (Wiersma et al., 2005). Basal metabolic rate

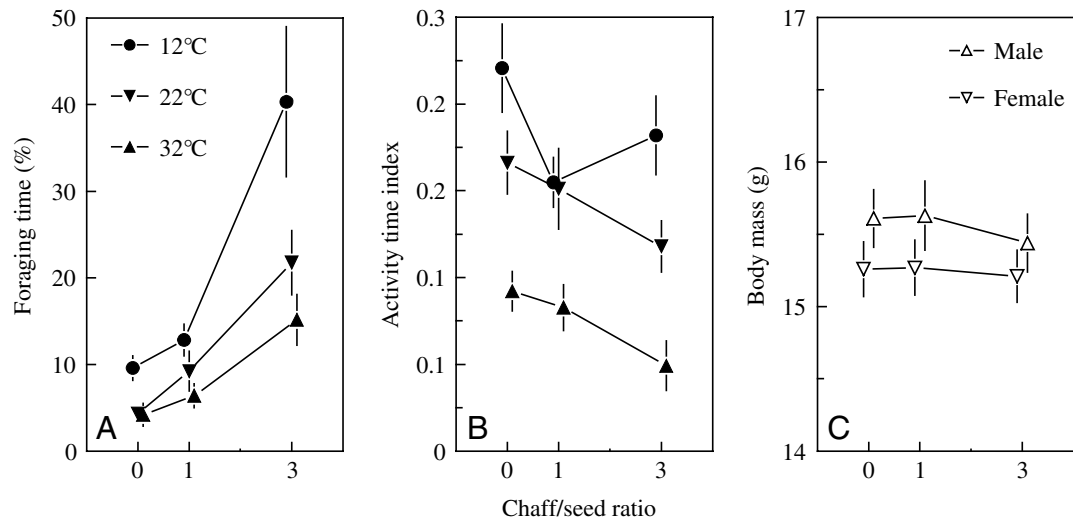


Fig. 1. Foraging time, activity and body mass in relation to chaff/seed ratio. (A) Proportion of time spent foraging between 09:00 h and 10:30 h increased with chaff/seed ratio ($F_{1,77}=22.0$, $P<0.001$), decreased with body mass ($F_{1,80}=8.81$, $P<0.005$) and with the interaction between temperature and chaff/seed ratio ($F_{1,71}=16.2$, $P<0.001$; temperature: $F_{1,70}=0.5$, $P=0.5$). The plotted data are not corrected for body mass. (B) Time spent on activities (including foraging) during the observation period was related to temperature ($F_{1,84}=39.2$, $P<0.001$) and chaff/seed ratio ($F_{1,84}=5.29$, $P=0.024$). (C) Body mass was independent of chaff/seed ratio (GLMM: $F_{1,169}=2.23$, $P=0.14$, including individual as random effect).

(BMR; Fig. 4), estimated by the minimum nocturnal values measured at 32°C, was not significantly related to chaff/seed ratio. However, at lower ambient temperatures minimum

nocturnal values of MR were negatively correlated with chaff/seed ratio, and there was a significant interaction between temperature and chaff/seed ratio (Fig. 4). The same results emerged when metabolic rate was expressed per gram (Fig. 4;

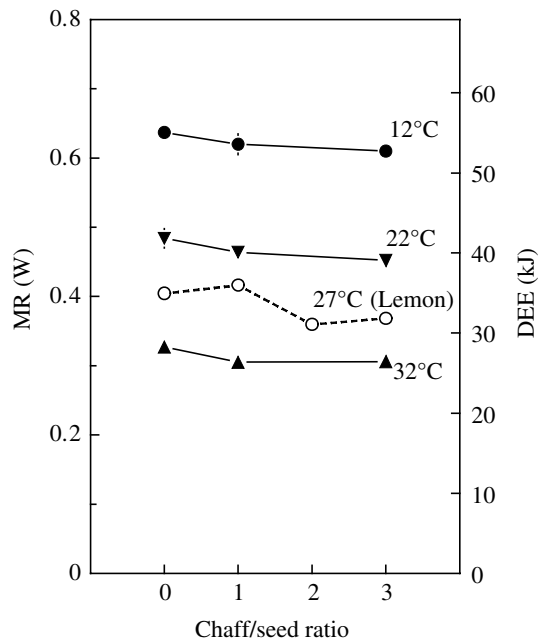


Fig. 2. Metabolic rate (MR in W) and daily energy expenditure (DEE in kJ) during a 24 h period declined with increasing chaff/seed ratio ($F_{1,85}=22.7$, $P<0.001$) and temperature ($F_{1,85}=3057$, $P<0.001$), and increased with body mass ($F_{1,93}=9.77$, $P<0.005$). The interaction between chaff/seed ratio and ambient temperature was not significant ($F_{1,84}=1.41$, $P=0.24$). Also plotted is the metabolizable energy intake as measured by Lemon (1993) in zebra finches on similar chaff/seed regimes. The plotted data are not corrected for body mass.

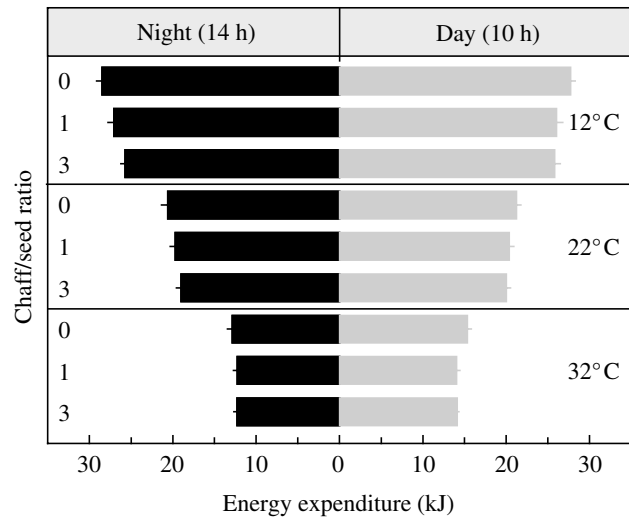


Fig. 3. Nocturnal and diurnal energy expenditure in relation to chaff/seed ratio and ambient temperature. Nocturnal energy expenditure ($\text{kJ } 14 \text{ h}^{-1}$) was negatively related to temperature ($F_{1,84}=1393$, $P<0.001$) and chaff/seed ratio ($F_{1,84}=22.0$, $P<0.001$), and positively to their interaction ($F_{1,84}=5.74$, $P=0.019$) and body mass ($F_{1,93}=11.8$, $P<0.001$). Diurnal energy expenditure ($\text{kJ } 10 \text{ h}^{-1}$) was negatively related to chaff/seed ratio ($F_{1,85}=15.5$, $P<0.001$) and temperature ($F_{1,85}=2265$, $P<0.001$) and positively to body mass ($F_{1,93}=5.83$, $P=0.018$), and there was no interaction between temperature and chaff/seed ratio ($F_{1,84}=0.13$, $P=0.72$). The plotted data are not corrected for body mass. Values are means \pm S.E.M. ($N=12$).

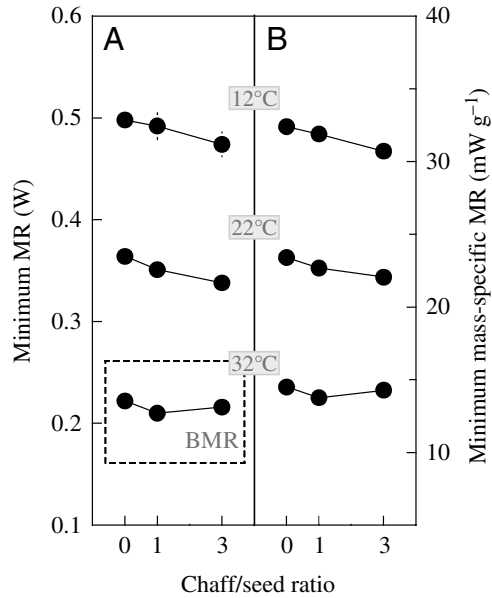


Fig. 4. Minimum values of metabolic rate (MR) measured during the night. (A) Minimum MR was negatively related to chaff/seed ratio ($F_{1,84}=16.1$, $P<0.001$) and temperature ($F_{1,84}=1278$, $P<0.001$) and positively to their interaction ($F_{1,84}=5.28$, $P=0.024$) and body mass ($F_{1,84}=8.69$, $P<0.005$). BMR (values at 32°C; Calder, 1964) was not related to chaff/seed ratio ($F_{1,23}=0.26$, $P=0.62$). The plotted data are not corrected for body mass. (B) Minimum values of mass-specific metabolic rates. Mass-specific MR was negatively related to chaff/seed ratio ($F_{1,85}=12.9$, $P<0.001$) and temperature ($F_{1,85}=1253$, $P<0.001$) and positively with their interaction ($F_{1,85}=4.24$, $P=0.043$). Mass-specific BMR was not related to chaff/seed ratio ($F_{1,23}=0.02$, $P=0.89$).

note that these ratios are hard to interpret since changes can be due to MR, mass, body composition or combinations of these factors).

Experiment 2

Feather growth

In accordance with the results of the respirometry measurements (Fig. 2), food consumption in the home cages decreased significantly with increasing chaff/seed ratio ($F_{1,22}=19.5$, $P<0.001$; tested using cage as random effect to accommodate repeated measurements). Quantitatively, the effect was even stronger than in the respirometry measurements, with seed consumption (in $\text{g bird}^{-1} \text{ day}^{-1}$, mean \pm S.E.M.) decreasing from 4.38 ± 0.10 to 3.97 ± 0.10 to 3.51 ± 0.13 for chaff/seed ratio 0, 1 and 3, respectively. Thus seed consumption at the maximum chaff/seed ratio was decreased by 20%, considerably more than the 6.6% reduction observed at room temperature during the respirometry sessions. This may be due to the fact that in the holding cages the chaff/seed mixture was renewed every other day, while the respirometry sessions always started with a fresh mixture. The chaff/seed ratio increased over time because seeds were consumed; after 48 h the chaff/seed ratios had increased from 1 to 2.7 and from

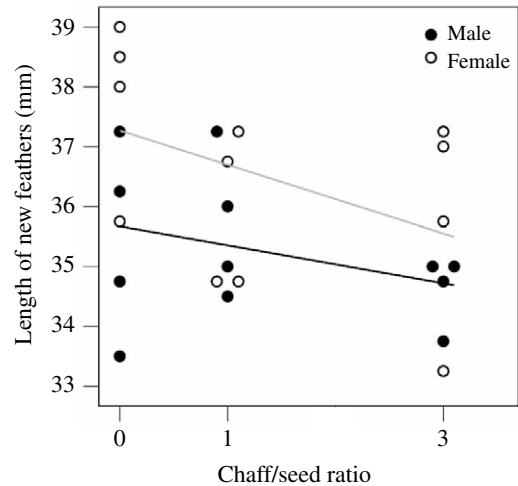


Fig. 5. Length of the new outer two tail feathers for birds maintained on different chaff/seed ratios. For P values, see text. Regression equations: female, $y=37.28-0.57x$ ($N=12$); male, $y=35.69-0.32x$ ($N=12$).

3 to 6.8 (excluding potential effects of the new chaff produced when consuming seeds).

The length of the newly formed feathers decreased with increasing chaff/seed ratio (Fig. 5; $F_{1,21}=3.77$, $P_1=0.03$; controlling for sex: $F_{1,21}=4.80$, $P=0.04$). The length difference between the extreme chaff/seed ratios was 1.4 mm (-4%). Controlling for length of the removed feather (which did not differ between treatments) did not change this result. Growth rates, expressed as the number of days until feather length reached 50% and 75% of its final length (calculated by interpolation), was independent of treatment ($F_{1,22}<1.14$, $P>0.7$).

Reproduction

Food intake rates during the 3 days after termination of the food manipulation tended to decrease over the course of those 3 days but, more importantly, food intake increased with the chaff/seed ratio experienced in the preceding 6 weeks, indicating that the birds were in a recuperating condition (Fig. 6).

When analyzing the effects of chaff/seed ratio on reproduction we controlled statistically for the feather removal experiment (as a dummy variable), which was done in half of the pairs. Three pairs (one in each group) did not produce any eggs, and were therefore excluded from the analyses. The distribution of the interval between the date that we offered nesting material and the first egg (the laying interval) was skewed to the left, and we ln-transformed the data prior to the analysis to normalize the error-distribution. Laying interval increased with chaff/seed ratio ($F_{1,18}=3.99$, $P_1=0.03$), and further inspection revealed that there was a significant interaction between chaff/seed ratio and feather removal (Fig. 7; $F_{1,17}=5.08$, $P<0.05$). Separate analyses confirmed that among the pairs where tail feathers were removed there was a significant effect of chaff/seed ratio on laying interval

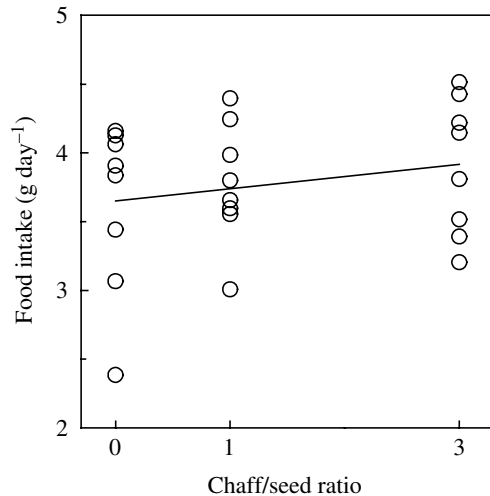


Fig. 6. Food intake ($\text{g bird}^{-1} \text{ day}^{-1}$) on days following the termination of the chaff/seed food regimes (i.e. all birds had seeds without chaff), in relation to the chaff/seed ratio experienced in the previous 6 weeks. Data points indicate the average over the 3 days per bird. Repeated measures GLM: chaff/seed ratio, $F_{2,21}=4.15$, $P=0.030$; day, $F_{2,21}=2.74$, $P=0.087$. Regression equation: $y=3.65+0.09x$.

($F_{1,8}=6.48$, $P_1<0.02$), while there was no such effect among birds where tails feathers were not removed ($F_{1,7}=0.01$, $P_1=0.5$). The difference between the groups is intriguing, because anecdotal information suggests that zebra finches have better reproduction after moulting, and these data suggest that replacement of a few feathers may be sufficient to induce such an effect. Lemon and Barth (1992) previously showed that the interval between two broods increased with increasing chaff/seed ratio, and our results demonstrate that this was at least in part due to carry-over effects of intake rate (and

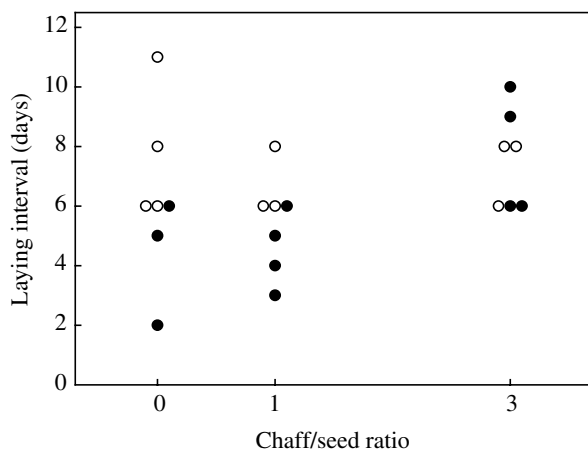


Fig. 7. Laying interval in relation to chaff/seed ratio in the six weeks preceding the day that nesting material was offered and all birds were given food without chaff. Laying interval was defined as the number of days between the day that nesting material was offered and the day the first egg was laid. Closed and open circles indicate pairs where feather were plucked or not plucked, respectively.

presumably the associated energy allocation) on their condition. Through unknown causes egg production was slightly irregular, and many eggs were infertile; we therefore restricted further analysis of reproduction to the total egg production over the 44 days following the day the birds were given breeding opportunities, at which point the first nestlings were close to fledging. Total egg production over this period was independent of chaff/seed ratio ($F_{1,18}=0.79$, $P=0.4$), and this did not change when summing egg production over different time intervals (e.g. the first 21 days). Egg mass (mean of all eggs a female produced) was also independent of chaff/seed ratio ($F_{1,18}=0.59$, $P=0.5$). Although far from significant, it is worth noting that the sign of the regressions for egg production and egg mass were both in the expected direction, i.e. lower for high chaff/seed ratios.

Discussion

Mixing the seeds with chaff considerably increased the time spent foraging. At the ambient temperature of the holding cages the foraging time increased from about 4% to 22% (Fig. 1: 22°C). However, this was not sufficient to compensate the decrease in intake rate because DEE decreased by 6.6% (Fig. 2: 22°C). In the holding cages the decrease in food consumption was even larger, with 20% lower food consumption at the highest chaff/seed ratio. Lemon (1993) also manipulated the intake rate of zebra finches by mixing seeds with chaff, and did not detect significant effects of chaff/seed ratio on DEE. However, his data were quantitatively in accordance with our results (Fig. 2), and lack of statistical significance in his study can probably be attributed to insufficient statistical power. The decrease in DEE was due to reductions in energy expenditure during both the diurnal and nocturnal periods (Fig. 3). At night, at 22°C, energy expenditure decreased by 7.7% and during the day by 5.6%. These effects were independent of body mass, because mass did not vary significantly with chaff/seed ratio (Fig. 1), and statistical significance of chaff/seed ratio remained when mass was included in the regression models.

The fact that DEE decreased with decreasing intake rate is surprising, because on the basis of simple theoretical considerations (see Introduction), and the results we obtained with starlings (see companion paper, Wiersma et al., 2005), an increase in DEE would be an intuitively more plausible pattern. Moreover, long-term training regimes in mammals generally result in an increase in RMR (Speakman and Selman, 2003), but birds may differ in this respect (Nudds and Bryant, 2001). In starlings, the effect of intake rate on DEE depended on whether a fixed or a variable foraging reward rate was applied; DEE decreased when intake rate was fixed but not when it was variable (Fotheringham, 1998). However, it seems unlikely that zebra finches foraging for seeds mixed with chaff experienced a fixed reward rate. To examine how our results compare to other studies we searched the literature for papers in which effects of manipulations of intake rate on activity and energy expenditure were reported, separating between

Table 1. Summary of results from experiments in which foraging reward rate was manipulated (without altering the predictability) in a closed economy system

	Reward rate	Foraging activity	Mass	Non-foraging activity	BMR or RMR	Daily food intake	DEE
Starling <i>Sturnus vulgaris</i> ¹	Variable	+	0	–		0	
Starling <i>Sturnus vulgaris</i> ²	Variable	+	–		–	+	+
Zebra finch <i>Taeniopygia guttata</i> ³	Variable	+	0			0*	0*
Zebra finch <i>Taeniopygia guttata</i> (this study)	Variable	+	0	–	0	–	–
Starling <i>Sturnus vulgaris</i> ¹	Fixed	+	–	–		–	
Starling <i>Sturnus vulgaris</i> ⁴	Fixed	+	–		–	–	–
Zebra finch <i>Taeniopygia guttata</i> ⁵	Fixed	+	–	(–)	–	–	–
Steely-vented hummingbird <i>Amazilia saucerrottei</i> ⁶	Fixed	+		–	–**	–	–
Fork-tailed emerald <i>Chlorostilbon canivetii</i> ⁶	Fixed	+		–	–**	–	–
Domestic pigeon <i>Columba livia</i> ⁷	Fixed	+	–		–***	–	
House mouse <i>Mus domesticus</i> ⁸	Fixed	0	0	–		–	
Deer mouse <i>Peromyscus maniculatus</i> ⁸	Fixed	0	0	–		–	
Siberian hamster <i>Phodopus sungorus</i> ⁹	Fixed	+	–			–	

The responses to a decrease in foraging reward rate are shown. Reward rates could either be fixed (without variation) or variable (only mean fixed). +, increases; –, decreases; 0, no change; indicators in parentheses refer to trends ($P < 0.1$).

*But note the quantitative agreement with our result of a negative effect in Fig. 2; **perching MR (not directly measured); ***inferred from body temperature.

¹Fotheringham (1998), ²Wiersma et al. (2005), ³Lemon and Barth (1992), ⁴Bautista et al. (1998), ⁵Deerenberg et al. (1998), ⁶Tiebout (1991), ⁷Rashotte and Henderson (1988), ⁸Perrigo (1987), ⁹Day and Bartness (2001).

experiments using variable and fixed reward rates (Table 1). In all studies foraging activity increased when foraging reward rate was decreased, except for one study of two rodent species where there was no significant change. However, despite the increase in foraging activity observed in most studies, only in our starling study (in which we used variable reward rates) did a decrease in reward rate result in an increase in DEE. In a comparable study of starlings that applied variable reward rates there was no effect of reward rate on food consumption (Fotheringham, 1998), probably because the range of reward rates was substantially smaller. Thus rather than increasing foraging effort to meet energy requirements, animals usually (10/13 studies) responded by consuming less energy. This was achieved firstly by reducing non-foraging activity (see also Wikelski et al., 1999), which was observed in all studies where this was quantified. Secondly, mass decreased in 50% of the studies, which yields a saving on maintenance costs. One way in which this bears out in the data is that BMR (or RMR) decreased in all studies where mass decreased. Note, however,

that the nocturnal energy saving observed in the present study could not be attributed to mass changes, possibly through mild hypothermia which is often observed when birds suffer food shortage (McKechnie and Lovegrove, 2002). Furthermore, independent of food access, exercise training results in lower RMR in zebra finches (Nudds and Bryant, 2001). Overall there does appear to be a difference between studies applying fixed and variable reward rates. DEE (or food consumption) decreased in all studies that used fixed reward rates, and some of these effects were quite strong (e.g. Deerenberg et al., 1998; Bautista et al., 1998), while DEE decreased in only one out of four studies that applied variable reward rates. This one exception is the present study, and why zebra finches responded in this way remains unresolved.

Foraging and food consumption under natural conditions is associated with the risk of being depredated or parasitized, suggesting there are benefits associated with low energy expenditure. An important question emerging is therefore why birds do not always save energy, given that the results listed in

Table 1 provide abundant evidence that this is a realistic option. We explored the hypothesis that animals save energy at the expense of somatic maintenance, thereby reducing fitness, which would explain why such savings are foregone in benign conditions. The length of replacement feathers decreased with increasing chaff/seed ratio (Fig. 5), in agreement with this hypothesis. This effect might have been caused by differences in growth rate (although we could not detect this), shape of the growth curves or length of the growth period, or a combination. Although this measure of somatic repair confirms our hypothesis, it is not known to what extent feather replacement is representative of all somatic repair processes. It is important therefore that chaff/seed ratio also had an effect on reproduction, in particular the laying interval (Fig. 7). Thus energy saving is an option for surviving periods in which foraging conditions are poor, but it is done at the expense of condition, which may explain why metabolic rates are generally higher than would be necessary for short-term survival alone.

We are very grateful to Tiede Swart and Yvonne Verkuil for practical assistance, and to the animal care takers, Sjoerd Veenstra, Roelie Veenstra-Wiegman and Tosca Boéré for maintenance of the zebra finches. Gerard Overkamp supported us by maintaining the respirometer and giving technical assistance when needed. Rudi Drent and Yvonne Verkuil provided comments on the manuscript. This study was carried out under license 2281 of the Animal Experiments Committee of the University of Groningen. S.V. was supported by NWO-SLW grant 803-30.165, an NWO-Vici grant, and the Technology Foundation STW (applied science division of NWO).

References

- Bautista, L. M., Tinbergen, J., Wiersma, P. and Kacelnik, A. (1998). Optimal foraging and beyond: How starlings cope with changes in food availability. *Am. Nat.* **152**, 543-561.
- Brody, S. (1945). *Bioenergetics and Growth*. New York: Hafner.
- Calder, W. A. (1964). Gaseous metabolism and water relations of the zebra finch, *Taeniopygia castanotis*. *Physiol. Zool.* **37**, 400-413.
- Day, D. E. and Bartness, T. J. (2001). Effects of foraging effort on body fat and food hoarding in Siberian hamsters. *J. Exp. Zool.* **289**, 162-171.
- Deerenberg, C. and Overkamp, G. J. F. (1999). Hard work impinges on fitness: an experimental study with zebra finches. *Anim. Behav.* **58**, 173-179.
- Deerenberg, C., Overkamp, G. J. F., Visser, G. H. and Daan, S. (1998). Compensation in resting metabolism for experimentally increased activity. *J. Comp. Physiol. B* **168**, 507-512.
- Finch, C. E. (1990). *Longevity, Senescence, and the Genome*. Chicago: The University of Chicago Press.
- Fotheringham, J. R. (1998). Starlings working for food in a closed economy: empirical studies of feeding regulation. PhD thesis, Oxford University, UK.
- Grubb, T. C., Jr, Waite, T. A. and Wiseman, A. J. (1991). Ptilochronology: induced feather growth in Northern cardinals varies with age, sex, ambient temperature, and day length. *Wilson Bull.* **103**, 435-445.
- Jenkins, K. D., Hawley, D. M., Farabaugh, C. S. and Cristol, D. A. (2001). Ptilochronology reveals differences in condition of captive white-throated sparrows. *Condor* **103**, 579-586.
- Kacelnik, A. and Bateson, M. (1996). Risky theories – The effects of variance on foraging decisions. *Am. Zool.* **36**, 402-434.
- Lemon, W. C. (1991). Fitness consequences of foraging behaviour in the zebra finch. *Nature* **352**, 153-155.
- Lemon, W. C. (1993). The energetics of lifetime reproductive success in the zebra finch *Taeniopygia guttata*. *Physiol. Zool.* **66**, 946-963.
- Lemon, W. C. and Barth, R. H. J. (1992). The effects of feeding rate on reproductive success in the zebra finch, *Taeniopygia guttata*. *Anim. Behav.* **44**, 851-857.
- Levy, A. (1964). The accuracy of the bubble meter method for gas flow measurements. *J. Sci. Instr.* **41**, 449-453.
- McKechnie, A. E. and Lovegrove, B. G. (2002). Avian facultative hypothermic responses: a review. *Condor* **104**, 705-724.
- Nilsson, J.-Å., Källander, H. and Persson, O. (1993). A prudent hoarder: effects of long-term hoarding in the European nuthatch, *Sitta europaea*. *Behav. Ecol.* **4**, 369-373.
- Nudds, R. L. and Bryant, D. M. (2001). Exercise training lowers the resting metabolic rate of zebra finches, *Taeniopygia guttata*. *Funct. Ecol.* **15**, 458-464.
- Perrigo, G. (1987). Breeding and feeding strategies in deer mice and house mice when females are challenged to work for their food. *Anim. Behav.* **35**, 1298-1316.
- Rashotte, M. E. and Henderson, D. (1988). Coping with rising food costs in a closed economy: feeding behaviour and nocturnal hypothermia in pigeons. *J. Exp. Anal. Behav.* **50**, 441-456.
- Speakman, J. R. and Selman, C. (2003). Physical activity and resting metabolic rate. *Proc. Nutr. Soc.* **62**, 1-14.
- Spencer, K. A., Buchanan, K. L., Goldsmith, A. R. and Catchpole, C. K. (2003). Song as an honest signal of developmental stress in the zebra finch (*Taeniopygia guttata*). *Horm. Behav.* **44**, 132-139.
- Tiebout, H. M., III (1991). Daytime energy management by tropical hummingbirds: responses to foraging constraint. *Ecology* **72**, 839-851.
- Verhulst, S., Riedstra, B. and Wiersma, P. (2005). Brood size and immunity costs in zebra finches. *J. Avian Biol.* **36**, 22-30.
- Vézina, F. and Williams, T. D. (2005). The metabolic cost of egg production is repeatable. *J. Exp. Biol.* **208**, 2533-2538.
- White, D. W., Kennedy, E. D. and Stouffer, P. C. (1991). Feather regrowth in female European starlings rearing broods of different sizes. *Auk* **108**, 889-895.
- Wiersma, P., Selman, C., Speakman, J. R. and Verhulst, S. (2004). Birds sacrifice oxidative protection for reproduction. *Proc. Biol. Lett.* **271**, S360-S363.
- Wiersma, P., Salomons, H. M. and Verhulst, S. (2005). Metabolic adjustments to increasing foraging costs of starlings in a closed economy. *J. Exp. Biol.* **208**, 4099-4108.
- Wikelski, M., Lynn, S., Breuner, C., Wingfield, J. C. and Kenagy, G. J. (1999). Energy metabolism, testosterone and corticosterone in white-crowned sparrows. *J. Comp. Physiol. A* **185**, 463-470.